JOURNAL OF FOREST SCIENCE, *62*, 2016 (7): 306–313

doi: 10.17221/118/2015-JFS

Effects of different irradiance levels on peroxidase activities in *Quercus castaneifolia* C.A. Mey. seedlings from different provenances

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ABSTRACT: To understand the function of peroxidase (POD) in relation to a light gradient, changes in POD activity were studied in five different provenances of chestnut oak seedlings. An experiment was conducted in controlled conditions and six different irradiances (10, 20, 30, 50, 60, and 70% of full light) were considered. According to the results, POD activity was strongly related to irradiance and showed a decreasing response to light, with the largest changes at low light (10 to 30%) and a levelling-off at high light (50–70%). Five provenances were also significantly distinguished at 10–30% of full light. The gel analysis showed that there were several different bands between irradiances from 10 to 70% regardless of provenances. One isoenzyme with the highest electrophoretic mobility was significantly increased in response to reduced light and slightly decreased at high irradiance. Other isoenzymes were significantly increased at high irradiance, suggesting that these isoenzymes are most likely involved in response to light stress and leaf adaptation to high irradiance.

Keywords: Hyrcanian vegetation zone; abiotic stress; polyacrylamide gel electrophoresis

Reactive oxygen species (ROS) are highly toxic to plant tissues and cause oxidative stress. Examples include both free radical ($O_2^{\bullet-}$, $OH^{\bullet}$, $HO_2^{\bullet}$, and $RO^{\bullet}$) and non-free radical forms (H_2O_2 and $^1O_2$) (Gill, Tuteja 2010). ROS cause damage to proteins, lipids, DNA, and carbohydrates. They also control many processes like plant growth, programmed cell death, abiotic stress responses, and pathogen defence by influencing the expression of a number of genes (Hansen et al. 2002; Gill, Tuteja 2010). Unfavourable conditions such as excess light (Hansen et al. 2002), drought, and salt stress (Wang et al. 2007) enhance the production of ROS in chloroplasts. In contrast, plants possess protective systems against oxidative stress damage, such as enzymatic and non-enzymatic antioxidants which scavenge ROS from the cells (Foyer, Noctor 2005). Peroxidases (PODs) are a variety of enzymatic antioxidant defence systems that include a large family of enzymes. For many of these enzymes, the optimal substrate is hydrogen peroxide. Lignification, suberization, auxin metabolism, cross-linking of cell wall proteins, defence against pathogen attack, salt tolerance, and oxidative stress are some physiological processes which are implicated by PODs (Gill, Tuteja 2010).

The light which filtered through the forest canopy could influence plant physiology and biochemical activity. Some studies have shown that excess light enhances the production of ROS and subsequently POD activity in chloroplasts (Hansen et al. 2002; Gill, Tuteja 2010).

Chloroplasts and peroxisomes are the main source of ROS generation in the light, but in the darkness, the mitochondria appear to be the main ROS producers. It was found that about 1 to 5% of the O_2 consumption of isolated mitochondria results in ROS production (Gill, Tuteja 2010). The concern of this study is to show the POD response to a light gradient in chestnut oak (*Quercus castaneifolia* C.A. Meyer). Chestnut oak is one of the most valuable species in Hyrcanian forests and is endemic in the Caucasian

vegetation zone (Akhani et al. 2010). This species is a light-demanding deciduous tree, distributed either in pure (4.6% of Hyrcanian forests) or in mixed populations (1.9%) with hornbeam (*Carpinus betulus* L.) from the coastal plains to the highlands along the southern shore of the Caspian Sea from west to east (Sabeti 1994). The results of the growth response of different provenances of chestnut oak seedlings to a light regime showed that attaining the maximal biomass varies across provenances and irradiance gradient (Soustani et al. 2014). Hence, it is possible that different provenances exhibit different quantitative and qualitative activities to a light gradient which may be the result of genetic adaptation to ecological conditions prevailing in the native habitat.

Although there are many studies on POD qualitative and quantitative activities to light, there are no studies on POD response to a light gradient. It is well established that the POD activity in plant cells is often regulated by both abiotic and biotic stresses. But the complexity of the physiological processes in which POD isoenzymes are involved makes it difficult to understand the specific function of each of these enzymes. Hence, an experiment in controlled conditions was conducted to understand how POD responds to a light gradient. The results will help to show critical light intensities for a single species and assist in planning applications of nature-based management of oak forests.

MATERIAL AND METHODS

Descriptions of collected provenances. To conduct this study, five provenances of chestnut oak were collected in the form of seeds along the precipitation gradient from west to east of the Hyrcanian forests (from 2,045 mm in the west to 488 mm in the east). General characteristics of the studied sites are shown in Table 1. This experiment was conducted in a greenhouse at the Faculty of Natural Resources and Marine Sciences of Tarbiat Modares University, situated within the Hyrcanian forests (36°34'54''N, 52°2'32''E, –22 m a.s.l.) in Mazandaran province (north of Iran).

Light regime treatment. To study the POD activity of chestnut oak seedlings to a light regime, six different irradiances, i.e. 10, 20, 30, 50, 60, and 70%, were considered. The inner space of the greenhouse was divided into six parts (as shade houses). Each part was approximately 3.5 m long by 1.5 m wide and 2.2 m high. Then, the six specified irradiances were provided by covering the walls of the shade houses using layers of neutral plastic, polyethylene, which transfers 90% of full light, and covering the roofs with an increasing number of layers of neutral shade. Each extra layer intercepted 10% of the incoming light. Each irradiance level contained 150 oak seedlings from five provenances (30 seedlings were placed randomly in the treatment for each provenance), plus 40 cm buffer at each of the north and south ends to avoid edge effects. Photosynthetically active radiation measurements were done in the shade houses based on comparisons of treatment vs. open sky instantaneous readings performed at noon at seedling height with an "SA type" spherical quantum sensor (LI-COR, Lincoln, USA) (Bloor, Grubb 2004) (Table 2).

Plant material. Chestnut oak acorns were collected from about 10 to 15 matured trees situated in five provenances and were sown in plastic pots (15 × 10 cm) filled with a mixture of one-third of forest top soil and two-thirds of river sand, in the autumn 2011. The source of the forest soil was from

Table 1. Characteristics of studied sites (Domores et al. 1998; Akhani et al. 2010; Pilembera – western provenance, Kelardasht, Lajim – central provenances, Kordkûy and Loveh – eastern provenances)

Province	Provenance	Altitude (m a.s.l.)	Coordinates	Temperature* (°C)	Precipitation* (mm)	Number of seeds·kg^{-1}	Number of trees per site
Guilan	Pilembera	650	37°34'25''N 49°1'40''E	15.1	2,045	185	15
Mazandaran	Kelardasht	1,000	36°35'52''N 51°5'30''E	16.4	1,293	125	10
	Lajim	800	36°18'22''N 53°5'48''E	18.0	703	138	15
Golestan	Kordkûy	800	36°43'27''N 54°7'21''E	17.8	601	135	12
	Loveh	800	37°21'11''N 55°39'44''E	17.8	488	135	14

*annual mean

Table 2. Rank order of the treatments based on comparisons of treatment vs. open sky instantaneous readings done at noon at seedling height with an "SA type" spherical quantum sensor (LI-COR, Lincoln, USA) (Bloor, Grubb 2004)

Irradiance treatment (%)	PAR (% of full daylight ± SE)
70	70.40* ± 2.29
60	57.19 ± 2.21
50	49.12 ± 2.39
30	31.17 ± 3.42
20	19.62 ± 3.23
10	11.02 ± 0.56

*mean of 5 replicates ± SE, PAR – photosynthetically active radiation, SE – standard error

the oak forest region near the study site. The forest soil was used to provide a substrate with the natural composition of macro- and micronutrients and the river sand provided a texture with adequate drainage, which allowed for daily watering of the seedlings. The temperature in the greenhouse was maximally at 26°C and minimally at 17°C and the mean relative air humidity inside the greenhouse was 77%.

After germination in the spring from late March to early April 2012, seedlings were positioned at a 10% irradiance level. By 1 May 2012, the seedlings were set up under light regime treatments. Moving the seedlings to higher irradiance was carried out gradually to avoid bleaching in response to the transfer and they were watered twice weekly. In this experiment, the average time for moving the seedlings to higher irradiance was two to three weeks (15 to 20 days).

Leaf sampling. Leaf sampling was carried out from 23 to 25 August, 2012 on three randomly selected individuals per provenance (15 seedlings for each shade house). The samples were placed separately in individual bags, conserved in a portable refrigerator and stored at 4°C until enzyme extraction. For the enzyme extraction, leaf tissue was crushed separately using a mortar and pestle and the enzyme was extracted using extraction buffer: 1 g of the seedling leaf was ground separately with 3 ml of extraction buffer (2 g ascorbic acid, 3.8 g borax (decahydrate), 50 g polyethylene glycol, 1.2 g tris-hydrochloride, 2 g ethylenediaminetetraacetic acid disodium salt dihydrate, and 3.6 g NaCl) and stored at 4°C in a refrigerator for 24 h. After centrifugation (3,000 g for 20 min at 4°C), extracts were stored at –20°C until they were used for electrophoresis (Kororı 1989).

Peroxidase activity was determined spectrophotometrically at the 530 nm wavelength with 0.01M acetate buffer A and B (1:1) 0.2 ml, 3% H_2O_2 0.4 ml, 0.01M benzidine 0.2 ml as reagent solution and the increase in A_{420} was recorded in 20 s (Kororı 1989). Electrophoresis was performed in vertical polyacrylamide gels (Petrokas, Stanys 2008). For isozyme analysis, about 30 µl of the extract of each sample was loaded into the well (the resolving and stacking gels contained acrylamide 120 g, bis-acrylamide 2 g, and tris-acrylamide 45.6 g). These materials were buffered to pH 7. Protean™ I vertical slab gel electrophoresis (Bio-Rad, Hercules, USA) apparatus was employed using tris-glycine electrode buffer. A constant current of 45 mA per gel was applied after each run that took about 10 h to complete. Then, electrophoresis gels were removed and stained for peroxidase with a solution of acetate buffer 40 ml, B acetate buffer 40 ml, 0.02% M benzidine 4 ml supplemented with hydrogen peroxide (Petrokas, Stanys 2008) and placed on a shaker for 35 min, thereafter, gels were washed in distilled water.

For estimating the seedling dry weight, the seedling parts were oven-dried for 48 h at least at 70°C and were weighed (Poorter 1999).

A two-way analysis of variance was used to understand whether there is an interaction between irradiance and provenances on POD activity, where irradiance and provenances were the independent variables and POD activity was the dependent variable.

Mean values of variables were compared using Tukey's test. The least significant range for POD quantitative activity at $P = 0.05$ ($Tukey_\alpha$) was calculated using the following formula (Eq. 1):

$$Tukey_\alpha = q_{\alpha,\, t,\, df\,(E)} \times (\sqrt{MSE}/n) \quad (1)$$

where:

q – values obtained from the Tukey's table,

α – 0.05 or 0.01,

t – degree of freedom factor +1,

$df\,(E)$ – degree of freedom error,

MSE – mean square error,

n – number of treatment.

For an enzyme qualitative analysis, the relative mobility of POD isoenzymes (R_f) was determined from the 'runs' in polyacrylamide gels, as Eq. 2:

$$R_f = r_i \times R^{-1} \quad (2)$$

where:

r_i – distance from the starting point of a 'run' to the position of an isozyme,

R – distance from the starting point of a 'run' to the blue band of bromophenol at the bottom of the gels (Petrokas, Stanys 2008).

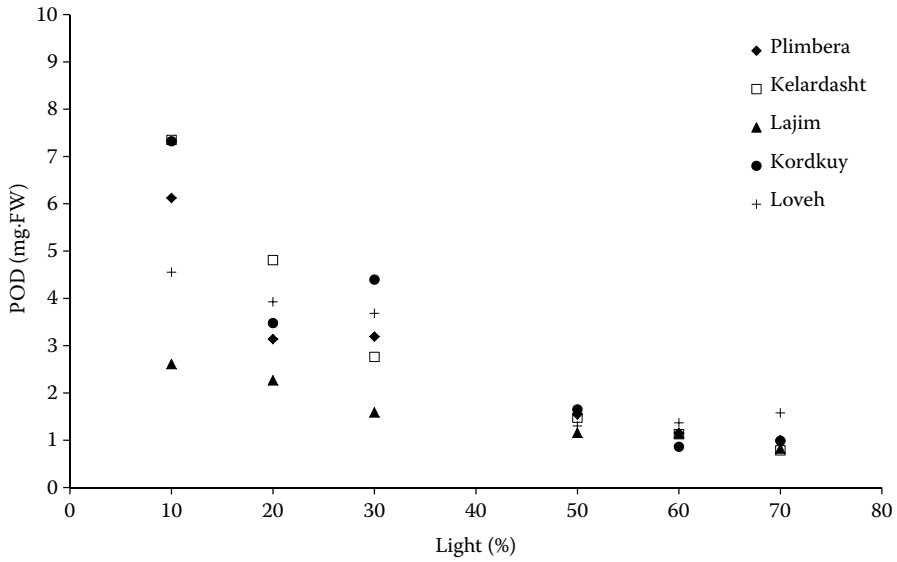

Fig. 1. Changes in peroxidase (POD) specific activity in five provenances of chestnut oak, the least significant range at $P = 0.05$

RESULTS

POD activity

To examine the functional responses to light, the averaged values for the POD specific activities were measured in five different provenances of chestnut oak (Fig. 1). Peroxidase activity showed a decreasing response to light, with the largest changes at the lowest irradiances (10–30%) and a levelling-off at higher irradiances (50–70%). As least significant range showed the provenances indicated a significant difference at 10–30%.

Irradiance was the most important determinant of variation in the POD activity, as shown by the high *F*-values (Table 3). Variation in POD activity due to light intensity ($R^2 = 0.36$) was much larger than variation due to provenances ($R^2 = 0.04$) or the interaction between provenances and light levels ($R^2 = 0.14$) (Table 3).

Analysis of POD isozymes

To show that POD isoenzymes are involved in the increase of POD activity at low irradiance, protein samples (which were extracted from leaves at 10 to 70% irradiance) were electrophoresed on polyacrylamide gels and POD isoenzymes were stained with staining solution (Fig. 2). The electrophoretic analysis showed that there were several different bands between irradiances from 10 to 70% regardless of the provenances. It seems that one isoenzyme with the highest electrophoretic mobility (marked with an arrowhead in Fig. 2 at $R_f = 0.15$) was significantly increased in response to reduced light, suggesting that this isoenzyme is most likely involved in low irradiance stress. This isoenzyme was not found at Lajim, which has the lowest levels of enzyme activity at low irradiances (Fig. 1). At high irradiance, this isoenzyme slightly decreases.

Other isoenzymes ($R_f = 0.4$ and 0.5) were significantly increased at high irradiance (marked with an arrowhead in Fig. 2), suggesting that these isoenzymes were involved in the adaptation of leaves to high irradiance.

In general, several specific bands of peroxidase were determined for the low and high irradiances ($R_f = 1.5$, 0.4, and 0.5) and POD band with R_f values of 0.2, 0.22, 0.6 and 0.65 was detected in all the provenances (Fig. 2). Thus, the results showed that the POD activity is strongly related to irradiance.

Growth response

Total biomasses obtained varied across provenances. Seedlings collected from the intermediate precipitation regimes (Kelardasht, Lajim, and

Table 3. Two-way analysis of variance with light ($n = 6$) and provenances ($n = 5$) as fixed factors, an equivalent for R^2 was calculated as the sum of squares of the effect in proportion to the total sum of squares

	POD activity		
	F-value	*P*	R^2
Provenance	10.39		0.04
Light	60.64	0.001	0.36
Interaction	5.92		0.14

POD – peroxidase

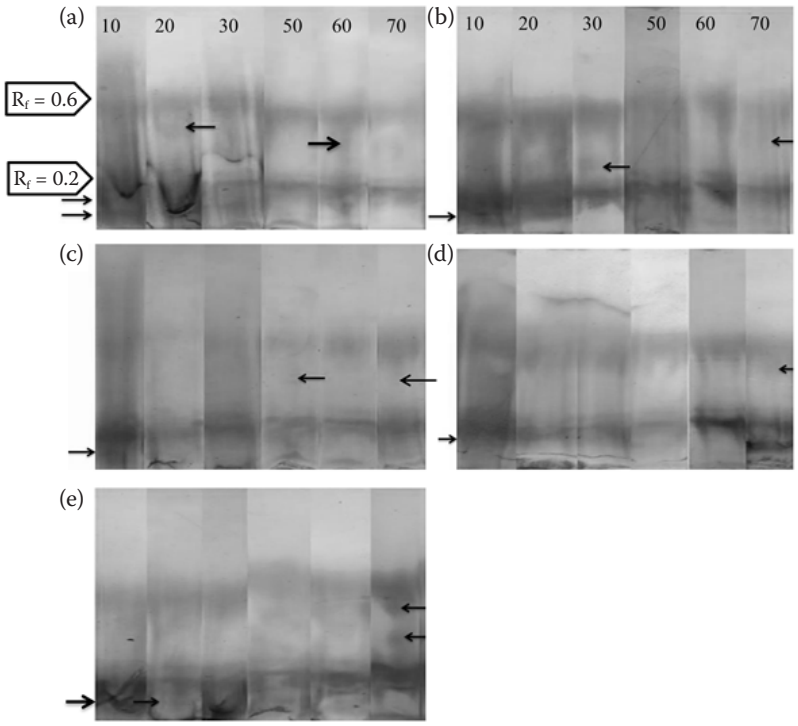

Fig. 2. Gel analysis for peroxidase activity in five provenances: Plimbera (a), Kordkûy (b), Kelardasht (c), Loveh (d), Lajim (e), of chestnut oak (*Quercus castaneifolia* C.A. Meyer) after exposure to six light levels (10–70%). 30 µl of samples were loaded on each gel and electrophoresis was conducted for 10 h, arrowheads indicate a novel isoenzyme induced by light

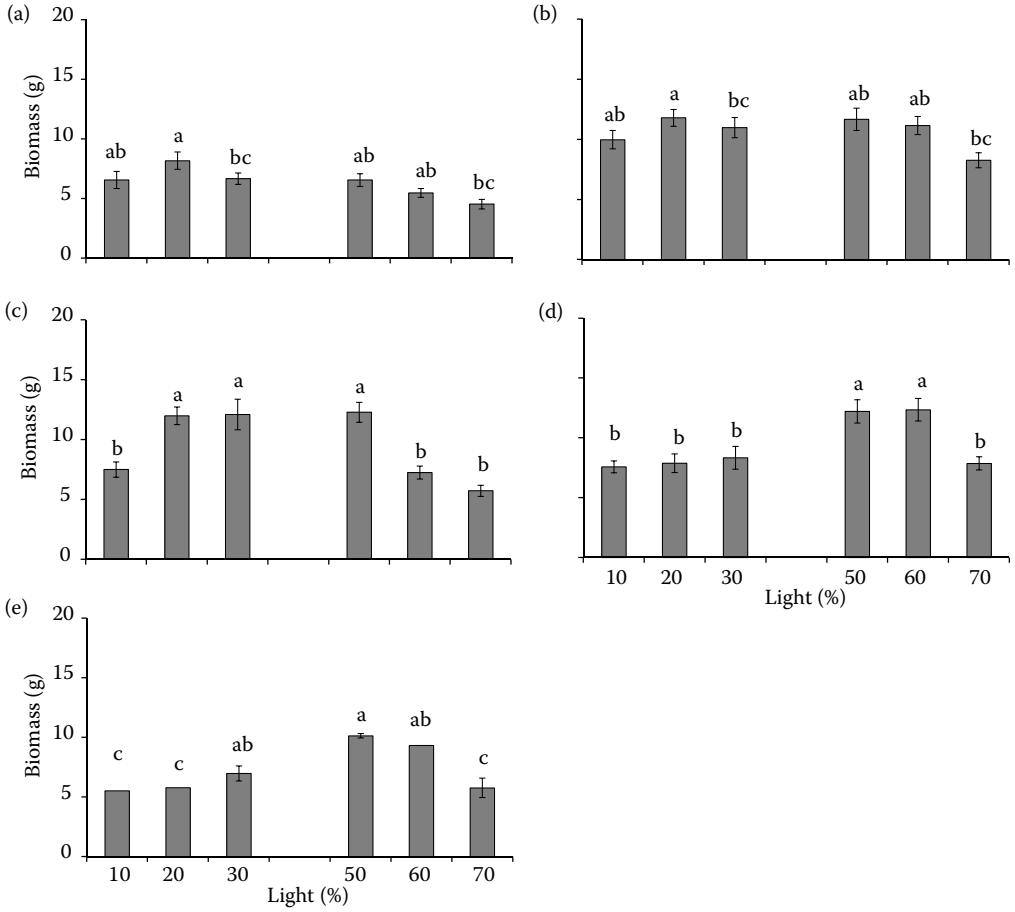

Fig. 3. Mean of the biomass (± SE) in different irradiance treatments (10–70%) for five provenances ($P < 0.05$): Plimbera (a), Kelardasht (b), Lajim (c), Kordkûy (d), Loveh (e)

Kordkûy) showed the highest biomass as compared to those from the highest (Plimbera) and lowest (Loveh) precipitation regions (Fig. 3). The biomasses obtained showed an optimal response at intermediate light levels. As shown in Fig. 3, it seems that the biomass obtained increased from wetter provenances to drier ones.

DISCUSSION

High light as unfavourable conditions can cause an increased production of ROS in plant tissues during photosynthesis and other reactions of cellular metabolism (Gill, Tuteja 2010). An increase in peroxidase activity has been considered as a protective system composed of antioxidants (Zolfaghari et al. 2010) showing that POD has been suggested to be involved in biotic and abiotic stresses. In this study, a close relationship was found between the POD specific activity and the relative light intensity, showing that the enzyme activity precisely reflects differences in the light environment especially at low irradiance (Fig. 1). POD activity was expected to increase from 10–70% irradiance, but the results showed a decreasing trend (Fig. 1). Peroxidase was high at low irradiance (10 to 30%), reached its lowest values at intermediate and high irradiance (at 50–70%). This result may be explained by considering that the chestnut oak is intermediate in shade tolerance (Rebbeck et al. 2012). An increase in the POD activity is symptomatic of oxidative stress. An increase in peroxidase activity was considered an early response to light stress and may provide cells with resistance against the formation of H_2O_2, which is formed when plants are exposed to stress factors (Zolfaghari et al. 2010).

Three main factors greatly determined the accumulation of ROS during stress: (*i*) balance between ROS production and scavenging (Mittler et al. 2004), (*ii*) the severity and the duration of the stress, (*iii*) the ability of the tissue to rapidly acclimate to the energy imbalance (Miller et al. 2010). Although peroxidase is a light-activated enzyme, the results of this study surprisingly showed that its activity increased upon low light treatment, whereas other studies showed that light caused a sharp rise in the enzyme activity (Reddy et al. 1985). The result of the present study is supported by the work of Begam and Vivekanandan (1990) that *Vigna unguiculata* (Linnaeus) Walpers showed an increase in POD activity upon low light treatment. They discussed the results in relation to the age of leaves. In this study, leaf sampling was investigated when the sampled seedlings had been set under light regime treatments for about four months. It seems that POD activity increases in mature leaves, which is in agreement with the findings of Begam and Vivekanandan (1990) and Moustaka et al. (2015).

The results showed that POD activity decreases in high light, but many studies showed that high light intensities were stressful for plants (Hansen et al. 2002; Kariola et al. 2005; Gill, Tuteja 2010). Prasad and Saradhi (2004) and Sofo et al. (2009) observed in their experiments that antioxidant enzymes decreased with an increase in the duration of exposure to intense light. Consequently, light intensity in sites with high light intensity may lead to an imbalance between the antioxidant defence and the amount of active oxygen species, thus resulting in more severe stress in physiology and ecology of seedlings.

Investigations to understand the function of each POD in terms of various biotic and abiotic stresses helped to identify a stress-induced promoter (Jang et al. 2004). The presence or absence of isoenzymes in response to stress showed that they are likely involved in a defence mechanism (Jang et al. 2004). In the present study, the presence of some isoenzymes at low irradiance and absence at high irradiance and conversely showed that some specific POD isoenzymes were involved in light stress in chestnut oak seedlings. It seems that one isoenzyme (R_f = 0.15) was significantly increased in response to reduced light, suggesting that this isoenzyme is most likely involved in low irradiance stress. Other isoenzymes (R_f = 0.4 and 0.5) were significantly increased at high irradiance (Fig. 1), suggesting that these isoenzymes were involved in leaf adaptation to high light. Gechev et al. (2003) revealed that one peroxidase isozyme was elevated by light. This may be related to the need for protection against light stress.

Peroxidase is a light activated enzyme and the results showed that POD activity is influenced by the light environment (Table 3). The enzyme analysis showed that five provenances were significantly distinguished at the given light-availability (10–30% levels). It may be demonstrated that different provenances from low to high precipitation regimes are different in light tolerance. The highest growth was related to Kelardasht, Lajim, and Kordkûy, which are intermediate in precipitation. It also seems that Lajim showed smaller oxidative stress than other provenances, probably because of the best function at an intermediate rainfall gradient. Increasing POD activity at low irradiance is considered a stress for all

provenances, but it seems that the growth strategies of chestnut oak seedlings are different in dry provenances as compared to wet provenances. Seedlings in wet provenances try to increase their biomass at low light (20–50%). In contrast, in dry provenances, seedlings increase biomass at 50–60%.

Despite similar growth conditions in the greenhouse, significant differences in POD activity and growth may be the result of genetic adaptation to the ecological conditions. When water availability increases along rainfall or topographical gradients, primary production increases, vegetation becomes denser, and light availability thus decreases. Species distribution along this combined water and light availability gradient is therefore largely determined by the species ability to tolerate drought and shade. Chestnut oak is considered to be intermediate in shade tolerance in the seedling stage (Rebbeck et al. 2012) and shows an optimal response at intermediate irradiance levels.

As noted earlier, it may be concluded that the POD light response curve can be used as an indicator of light tolerance of different provenances of chestnut oak seedlings. In general, according to the results, 50–60% of full light was suggested for the growth of *Q. castaneifolia* seedlings. But more investigations are needed, especially in natural environmental conditions.

Acknowledgement

The authors are grateful to S. Azizi, S. Gharemahmodli, M. Porreza, Dr. M. Matinizadeh, and T. Feyzi for their help with harvesting and supporting. B. Naseri is acknowledged for his help in collecting seeds.

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Received for publication December 20, 2015
Accepted after corrections June 7, 2016

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